A C T A P A R A S I T O L O G I C A P O L O N I C A
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Morphological adaptations of tapeworm eggs and their importance in the life cycles

Morfologiczne adaptacje jaj tasiemców i ich znaczenie w cyklach rozwojowych

The object of my investigations of several years were the life cycles of bird tapeworms from the orders *Anseriformes, Colymbiformes* and *Ralliformes* occurring in the lake districts of Northern Poland. In the course of these investigations I have determined the intermediate hosts for 28 tapeworm species and I have collected the material concerning the morphology of the live invasive eggs of those tapeworms.

The purpose of the present paper is to show whether and in what degree the shape and size of the eggs, different in various species, reflect the adaptation of the tapeworms to their developmental conditions. I am dealing with that problem on the basis of the life cycles of the tapeworms which I examined, by using the method of experimental invasion of intermediate hosts connected with parallel studies on the natural invasion of the intermediate hosts occurring in places of natural contacts with the final hosts.

It is with much pleasure that I take this opportunity of mentioning the name of the late Prof. Dr. W. L. Wiśniewski to whom I am indebted for the direction of my investigations and for enabling me the collection of the material for this paper.

At the same time I express my gratitude to Prof. Dr. W. Stefański who took care of my work after the death of Prof. Wiśniewski and who supplied me with precious suggestions while writing this paper.

I am also grateful to Prof. Dr. Z. Raabe for consulting the problems connected with adaptation of tapeworm eggs.

1. Methods

The investigation was carried out successively in three lakes of Northern Poland: Drużno in 1950—1951 and 1951, Gołdapiwo in 1954—55, and Mamry Północne 1956—1958.

The continual investigations in each of those lakes took place in summer (July, August, September) and in periods of ten days in May and November.

I searched for the intermediate hosts of tapeworms in two ways. On the one hand I examined the natural invasion of *Crustacea* occurring in places of their natural contacts with the final hosts. The results of those invesigations were presented in my preceding papers.

The second method was the experimental invasion. Eggs of tapeworms obtained from uterine segments were contacted with unispecies, small *Crustacea* cultures

(30 to 50 specimens). There was also attempted the invasion of *Gastropoda, Oligochaeta* and *Amphipoda* with tapeworm eggs to examine the life cycles of cestodes. It was also cared for the conditions of the experimentally invaded species of *Copepoda, Ostracoda* and *Cladocera* to be as close as possible to the conditions of their natural biotopes in the lake; therefore the lake-water with addition of slime or plants was used for the culture. It has to be mentioned that especially *Ostracoda* which have pretty specific biotopes in the lake, were very difficult to culture in the experimental conditions.

The essential factor in the experimental invasion was the maturity of eggs, i. e. the invasiveness of oncospheres. Eggs for the experimental invasion could be collected only artificially by squeezing them out of the uterine segments; thus they could be uninvasive, though they possessed formed oncospheres with embryonal hooks. Due to numerous experiments and observations, I found that the invasiveness of oncospheres was connected with the full development and maturity of egg membranes. Their maturity can be determined by observing them in water, i. e. in natural environment in which they have to accomplish one of their roles, i. e. a protection against the osmotic and mechanical action until the moment of swallowing the egg by the intermediate host.

When the membranes were not mature it happened that eggs were swelling and to the external membrane there were attaching different small particles present in water, and the disintegration processes of eggs could be already observed after some minutes or after some hours depending on the degree of their maturity. The ripe eggs, however, kept their shapes and dimensions in water for several or more than ten days.

The most certain criterion of the maturity of eggs was the passing of oncospheres into the body cavity.

2. Materials

The whole material concerning *Crustacea* which was examined to detect the natural invasion with tapeworm larvae, comprised more than 110 thousand specimens. I found in those crustaceans 512 cysticercoids belonging to 22 tapeworm species. A considerable material of the developmental stages of tapeworms came from the experimental invasions of crustaceans and other invertebrates with invasive eggs obtained from bird tapeworms.

The intermediate hosts of the majority of those tapeworms were not known so far. Owing to the investigations of Linstow 1892, Mrazek 1891 and Daday 1901, there were already known cysticercoids from naturally infected fresh-water invertebrates (*Copepoda, Ostracoda, Amphipoda, Gastropoda* and larvae of *Insecta*) but only for few of them: *Hymenolepis gracilis, Dicranotaenia coronula, Fimbriaria fasciolaris, Tatria acanthorhyncha*. Those authors determined the cysticercoids, which they found from natural invasion sporadically, by comparing their scolices with those of the adult tapeworms living in water birds.

Moreover, Joyeux et Baer 1950 obtained experimentally from among the tapeworms investigated by me, cysticercoids of *Drepanidotaenia bisacculina* in *Macrocyclops fuscus* (Jur.).

The whole material, descriptions, dimensions and drawings of cysticercoids and eggs have been given in separate publications (Jarecka 1958a, b, c, 1960).

Thus, as a result of an experimental invasion of invertebrates with the eggs of tapeworms and the investigations on their natural invasion, the intermediate hosts for the following tapeworm species were determined:

1. *Aploparaksis furcigera* (Rudolphi 1819).

Experimental invasion: *Limnodrillus* sp. (*Oligochaeta*) — Jarecka 1960a.

2. *Dicranotaenia coronula* (Dujardin 1845).

Experimental invasion: *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.), *Dolerocypris fasciata* (O.F.M.); negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.) — Jarecka 1958a, 1960.

Natural invasion: *Cyclocypris laevis* (O.F.M.) — Jarecka 1958a, 1960.
Natural invasion after Daday 1901, Joyeux et Baer 1930: *Cyclocypris laevis* (O.F.M.), *C. ovum* (Jur.), *C. globosa* Sars, *C. compressa* (Koch.), *C. dispersa* (Müll.), *Cypris cinerea* (Brady), *Potamocypris ophthalmica* (Jur.), *Eucypris viriens* (Jur.), *Candona candida* (O.F.M.).

3. *Drepanidotannia bisacculina* Szpotańska 1931.

Experimental invasion: *Macrocyclops fuscus* (Jur.) — Joyeux et Baer 1950. In my material this species was not invaded.
Natural invasion: *Acanthocypris viridis* (Jur.) — Jarecka 1960a.

4. *Diorchis nyrocae* Yamaguti 1935.

Experimental invasion: *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.); negative results: *Macrocyclops albidus* (Jur.) and *Acanthocyclops viridis* (Jur.) — Jarecka 1958a.
Natural invasion: *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.) — Jarecka 1958a.

5. *Diorchis inflata* (Rudolphi 1819).

Experimental invasion: *Cypridopsis vidua* (O.F.M.) — Rybicka 1957.
Natural invasion: *Cypridopsis vidua* (O.F.M.) — Jarecka 1958a, 1960.

6. *Diorchis parvogenitalis* Skrjabin et Mathevossian 1945.

Experimental invasion: *Cypridopsis vidua* (O.F.M.); negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Cyclocypris laevis* (O.F.M.) — Jarecka 1958a.

7. *Diorchis ransomi* Schultz 1940.

Experimental invasion: *Cypridopsis vidua* (O.F.M.) — Rybicka 1957.
Natural invasion: *Cyclocypris laevis* (O.F.M.), *Cypridopsis vidua* (O.F.M.) — Jarecka 1958a, 1960.

8. *Diorchis stefańskii* Czapliński 1956.

Experimental invasion: *Dolerocypris fasciata* (O.F.M.). In *Cypridopsis vidua* and *Notodromas monacha* the development of the oncospheres did not occur. Negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.), *Eucyclops macruroides* (Lill.), *Cyclocypris laevis* (O.F.M.) — Jarecka 1958a, 1960.

9. *Diploposthe laevis* (Bloch 1782).

Experimental invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.); the main intermediate host seems to be *Macrocyclops albidus*. Some cysticercoids developed also in *Cypridopsis vidua* — Jarecka 1958a.
Natural invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.) — Jarecka 1958a.

10. *Diploposthe sui-generis* Kowalewski 1903.

Experimental invasion: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.), and in a small degree (15%) *Cypridopsis vidua* (O.F.M.) and *Cyclocypris laevis* (O.F.M.). The main intermediate host seems to be *Macrocyclops albidus* (Jur.).
Natural invasion: Because the larvae of this species can not be differentiated from *D. laevis*, the intermediate hosts are given above — Jarecka 1958a (treated as *D. skrjabini* Mathevossian — Jarecka 1960).

11. *Echinocotyle clerci* Mathevossian et Krotov 1949.

Natural invasion: *Acanthocyclops viridis* (Jur.) — Jarecka 1958a.

12. *Echinocotyle drużniensis* Jarecka 1958.

Natural invasion: *Macrocyclops albidus* (Jur.), *Mesocyclops leuckarti* (Cl.), *Acanthocyclops viridis* (Jur.), *Eucyclops serrulatus* (Fisch.), *E. macruroides* (Lill.), *E. macrurus* (Sars), *Mesocyclops oithonoides* (Sars) — Jarecka 1958a.

13. *Echinocotyle rosseteri* Blanchard 1891.

Natural invasion: not determined *Ostracoda* species in the lake Drużno, and 2 *Radix ampla (Gastropoda)* — Jarecka 1958a.

14. *Fimbriaria fasciolaris* (Pallas 1781).

Experimental invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.). The main intermediate hosts are *M. albidus* and *A. viridis*.
Natural invasion: *Macrocyclops albidus* (Jur.), *Eucyclops serrulatus* (Fisch.), *Cyclocypris laevis* (O.F.M.) — Jarecka 1958a. Joyeux et Baer 1930 mention as the natural intermediate hosts: *Diaptomus vulgaris* Schm., *Cyclops* spp. Garkavi found the cysticercoids in *Gammarus* sp.

15. *Fimbriarioides intermedia* Fuhrmann 1913.

Experimental invasion: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.). The main intermediate host is *M. albidus*.
Natural invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Eucyclops serrulatus* (Fisch.) — Jarecka 1958a.

16. *Hymenolepis abortiva* (Linstow 1904).

Experimental invasion: *Gammarus* sp. — Jarecka 1960.

17. *Hymenolepis aequabilis* (Rudolphi 1810).

Experimental invasion: *Cyclocypris laevis* (O.F.M.).
Natural invasion: *Cyclocypris laevis* (O.F.M.) — Jarecka 1960.

18. *Hymenolepis compressa* (Linton 1892).

Experimental invasion: *Macrocyclops albidus* (Jur.), *Mesocyclops leuckarti* (Cl.).
Natural invasion: the same species — Jarecka 1958a, 1960.

19. *Hymenolepis gracilis* (Zeder 1803).

Experimental invasion: *Cypridopsis vidua* (O.F.M.), *Dolerocypris fasciata* (O.F.M.) — Jarecka 1958a.
Natural invasion: *Cypridopsis vidua* (O.F.M.), — Jarecka 1958a. Joyeux et Baer mention many species of *Copepoda* and *Ostracoda*.

20. *Hymenolepis furcifera* (Krabbe 1869).

Experimental invasion: *Simocephalus* sp., *Ceriodaphnia reticulata* Sars, *Eurycercus lamellatus* (100% invasion, 1 — 24 cysticercoids in one specimen). Negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.), *M. oithonoides* (Sars), *Eucyclops macrurus* (Sars), *E. macruroides* (Lill.), *Cyclocypris laevis* (O.F.M.), *Cypridopsis vidua* (O.F.M.), *Notodromas monacha* (O.F.M.) — Jarecka 1958a.
Natural invasion: *Eurycercus lamellatus* (O.F.M.) — Jarecka 1958b.

21. *Hymenolepis macrocephala* Fuhrmann 1913.

Experimental invasion: *Notodromas monacha* (O.F.M.). In *Cypridopsis vidua* the oncosphaerae reached the body cavity, but their further development did not occur. Negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Eucyclops macruroides* (Lill.), *Cyclocypris laevis* (O.F.M.).
Natural invasion: *Notodromas monacha* (O.F.M.) — Jarecka 1960.

22. *Hymenolepis megalops* (Creplin 1829).

Experimental invasion: *Cypris pubera* O.F.M.; negative results: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Cypridopsis vidua* (O.F.M.), *Notodromas monacha* (O.F.M.).
Natural invasion: *Cypris pubera* O.F.M. — Jarecka 1958a.

23. *Hymenolepis paracompressa* Czapliński 1956.

Experimental invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.). The main intermediate host is *M. albidus*.
Natural invasion: *Macrocyclops albidus* (Jur.), *Mesocyclops leuckarti* (Cl.), *Eucyclops serrulatus* (Fisch.), *E. macruroides* — Jarecka 1958a.
Beside, at the lake Drużno the cysticercoids of *H. paracompressa* occurred in naturally invaded snails, mainly in three species: *Radix ampla* Hartm., *R. ovata* Drap. and *R. auricularia L.* The intensivity of invasion was 1 — 20 cysticercoids in one specimen. Also other species were invaded in a small degree: *Limnaea stagnalis* L., *Amphipeplea gluteosa* Müll., *Stagnicola palustris* Müll., *Planorbis planorbis* L. and *Acroluxus lacustris* L.
To explain the role of snails, the experimental invasions were carried on; it was shown that *Gastropoda* are the reserve hosts (hote d'attende). The cysticercoids do not develop in them, but are stored in the intestine after the invaded *Copepoda* are swallowed. After beeing eaten by ducks, the snails create an additional way of the transfer of cysticercoids to the final hosts.

24. *Hymenolepis paramicrosoma* Gąsowska 1935.

Experimental invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.); negative results: *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.).
Natural invasion: *Macrocyclops albidus* (Jur.) — Jarecka 1958a.

25. *Hymenolepis sacciperium* Mayhew 1925.

Experimental invasion: *Cyclocypris laevis* (O.F.M.) in 45%, what shows that it is not a main intermediate host; negative results: *Macrocyclops albidus* (Jur.), *Cyclocypris laevis* (O.F.M.) — Jarecka 1960.

26. *Hymenolepis spiraliburstata* Czapliński 1956.

Experimental invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.).
Natural invasion: *Macrocyclops albidus* (Jur.), *Acanthocyclops viridis* (Jur.), *Mesocyclops leuckarti* (Cl.) — Jarecka 1958a. Also snails were invaded with the cysticercoids of *H. spiralibursata* at the Drużno lake: *Radix ampla* Hartm., *R. auriculata* L. and *R. ovata* Drap., and in a small degree: *Limnaea stagnalis* L. and *Anodonta piscinalis* Nils.

27. *Tatria acanthorhyncha* (Wedl 1855).

Experimental invasion: *Macrocyclops albidus* (Jur.) — Jarecka 1960. Linstow 1892 found this cysticercoid in a naturally invaded larva of *Agrion puella*.

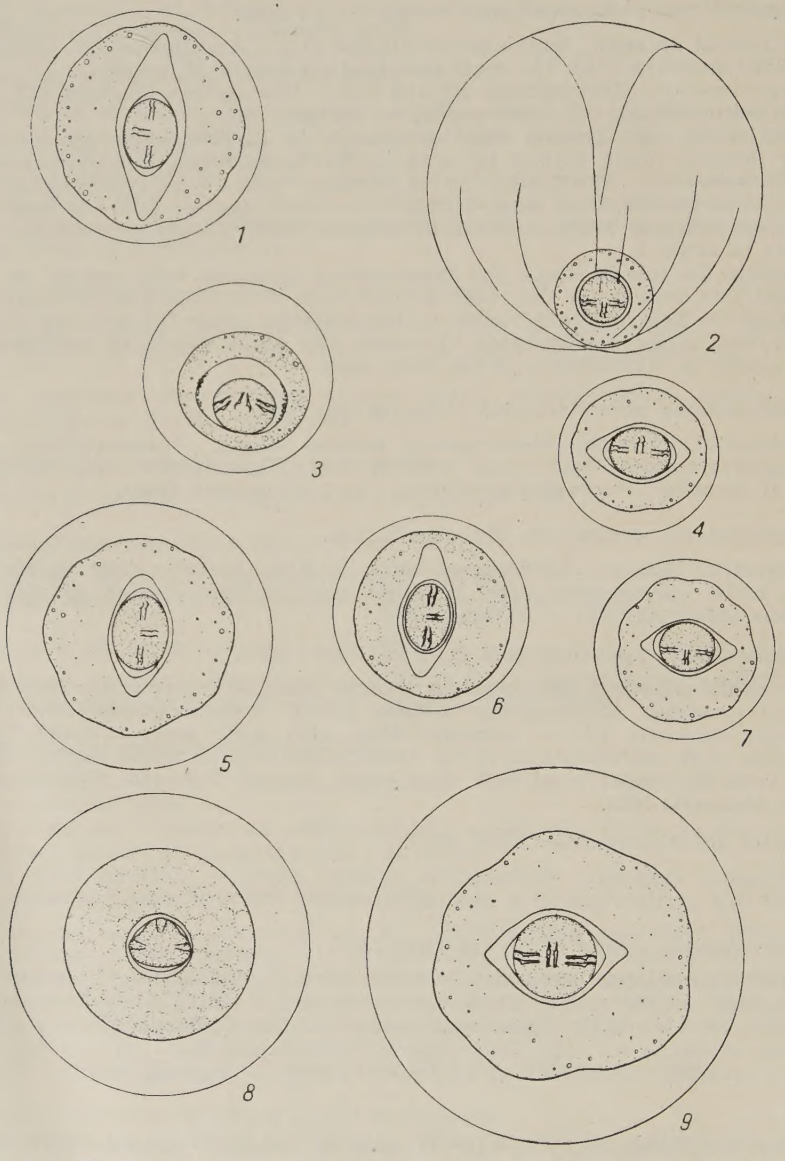
28. *Anomotaenia ciliata* (Fuhrmann 1913).

Negative experimental invasion: *Macrocyclops albidus* (Jur.), *M. fuscus* (Jur.), *Acanthocyclops viridis* (Jur.), *Eucyclops macruroides* (Lill.), *E. macrurus* (Sars), *Mesocyclops leuckarti* (Cl.), *Cypridopsis vidua* (O.F.M.), *Cyclocypris laevis* (O.F.M.), *Notodromas monacha* (O.F.M.), *Dolerocypris fasciata* (O.F.M.).
Natural invasion: *Simocephalus expinosus* (Hoch.) — Jarecka 1958a.

3. The morphology of live invasive eggs of the investigated tapeworms

The live invasive eggs of tapeworms, the life cycle of which is connected with the water environment, were not so far the object of special studies. The descriptions of eggs, usually given with the descriptions of tapeworms,

concern the preserved material where in the eggs crowded in uterus there is visible only the oncosphere and the shape of egg membranes deformed by fixation. In many cases those descriptions could concern the immature eggs, then, those eggs without well developed membranes.



Eggs of: 1 — *Fimbriarioides intermedia*; 2 — *Proteocephalus percae*; 3 — *Drepanidotaenia lanceolata* (after Ruszkowski 1932); 4 — *Hymenolepis spiralibursata*; 5 — *H. compressa*; 6 — *H. vistulae* (after Czapliński 1960); 7 — *H. paracompressa*; 8 — *Tatria acanthorhyncha;* 9 — *Diploposthe laevis*

As the descripti ns given by me concern live and mature eggs observed in water, i. e. in na ral environment, their detailed comparison with those given so far in literature would be aimless.

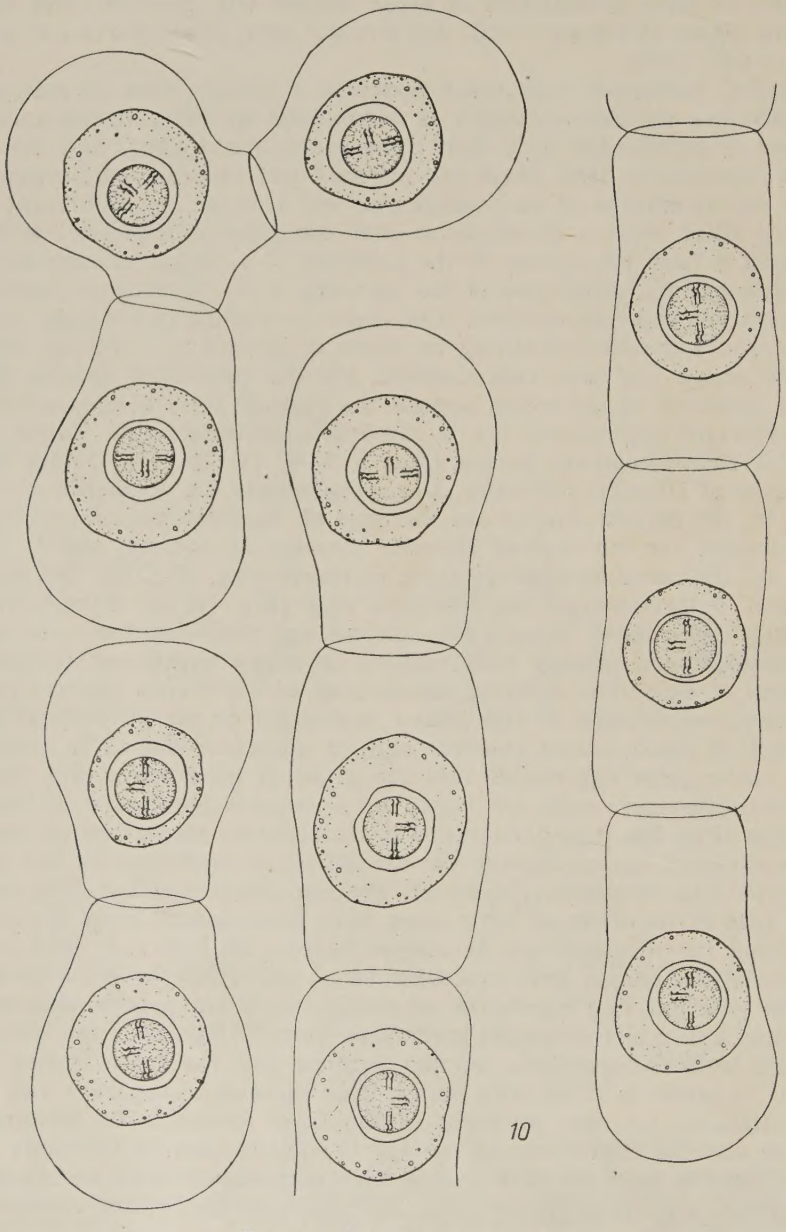
Presenting a general survey of egg morphology I base on the detailed descriptions given in my earlier publications concerning life cycles of tapeworms and on some publications of other authors who described live eggs of tapeworms (Ruszkowski 1932, Rybicka 1957, Belopolskaja 1958, Czapliński 1960).

In natural conditions eggs reach water in a mature state. A mature egg has an invasive oncosphere which is surrounded by three membranes. The oncosphere is surrounded by a thin transparent film which I call the membrane of oncosphere, then come the internal and external egg membranes. Between the membrane of oncosphere and the internal egg membrane there is a space filled with a structureless and transparent substance, what can bring about a false impression of the presence of a bigger number of mem-

The external egg membrane of the majority of the invesigated tapeworms is a transparent and fine outlined film which is crushed in the eggs crowded in the uterus, but when comming in water it spreads and the egg assumes a definite shape and size characteristic for the particular species. It can assume a spherical shape which possess the eggs of *Hymenolepis compressa, H. spiralibursata, Diploposthe laevis, Fimbriarioides intermedia, Tatria acanthorhyncha, Paricterotaenia porosa* (Fig. 1, 3—9, 19, 20—22). Ovally shaped are the eggs of *Diorchis stefańskii, D. parvogenitalis, Hymenolepis aequabilis* (Fig. 15, 16, 18); spindle-shaped are the eggs of *Anomotaenia ciliata* (Fig. 23); filiform-shaped are the eggs of *Diorchis nyrocae, D. ransomi* and *D. inflata* (Fig. 11, 13, 14); ramified eggs are those of *Diorchis* sp. (Fig. 12). The external membranes of *Hymenolepis macrocephala* eggs (Fig. 17) are irregularly oval and slightly disk-shaped. Finally the external egg membranes of some species are glued together, forming thus varying in shape permanent packets-like connections of eggs. The external membranes of *Fimbriaria fasciolaris* eggs, for instance, are cylindrical and joined in straight or curved cords (Fig. 10). The packet of *Hymenolepis abortiva* eggs is horseshoe-shaped in which the external rectangular egg membranes are glued at their edges (Fig. 25). The *Aploparaksis furcigera* eggs are joined by a common membrane in irregular little lumps (Fig. 26). It is probable that the common membrane in this case is not an external egg membrane but an additional membrane of the packet. The external egg membrane, however, are also glued together. The connections of eggs in the form of little stars have been described by Belopolskaja 1958 for *Anomotaenia paramicrorhyncha* Dubinina 1953, and in the form of little chains with processus for *A. platyrhyncha* Krabbe 1869.

As the external egg membrane of many tapeworm species observed by me becomes a thin and crumpled membrane immediately after the taking out of the eggs from the segments, we may suppose that the space formed by its stretching in water is filled with water. This space is transparent and structureless. Its size, i. e. the thickness of the layer between the internal egg membrane and the film covering the egg externally, can be different in various species. For example, it is thin in *Dicranotaenia coronula* and in *Hymenolepis gracilis* eggs (Fig. 19), or thick in *Diploposthe laevis*, and *Anomotaenia ciliata* eggs (Fig. 23).

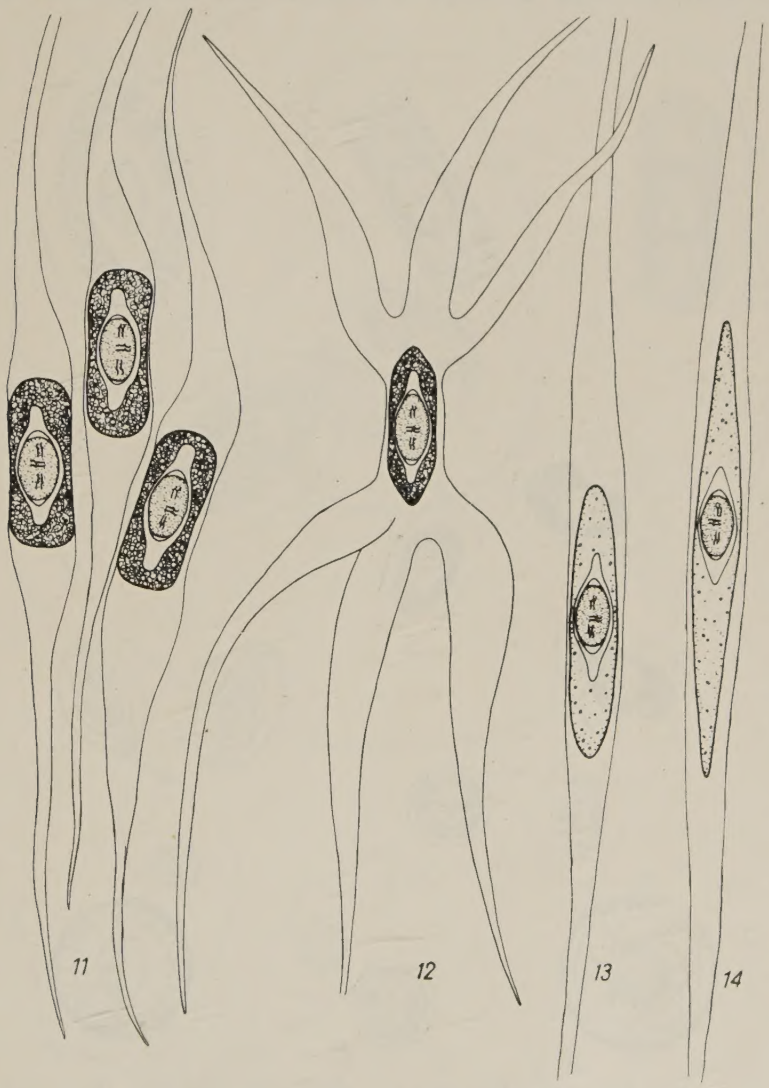
Speaking about the thickness of the external egg membrane I think of the outline of the external film which is compressed in the uterus. This film is very thin in eggs of some species and invisible by small microscopic magnifying, as for instance, in the eggs of *Anomotaenia ciliata*, *Hymenolepis furcifera*, and *H. macrocephala* (Fig. 17, 23, 24), and a bit thicker in the eggs



Eggs of *Fimbriaria fasciolaris*

of *H. compressa, H. spiralibursata* and in many others presented in the figures. On the other hand the eggs of *H. megalops* and *H. sacciperium* have the external egg membrane considerably thick, forming a kind of hard shell. Moreover, it adheres almost closely to the internal membrane (Fig. 20, 21).

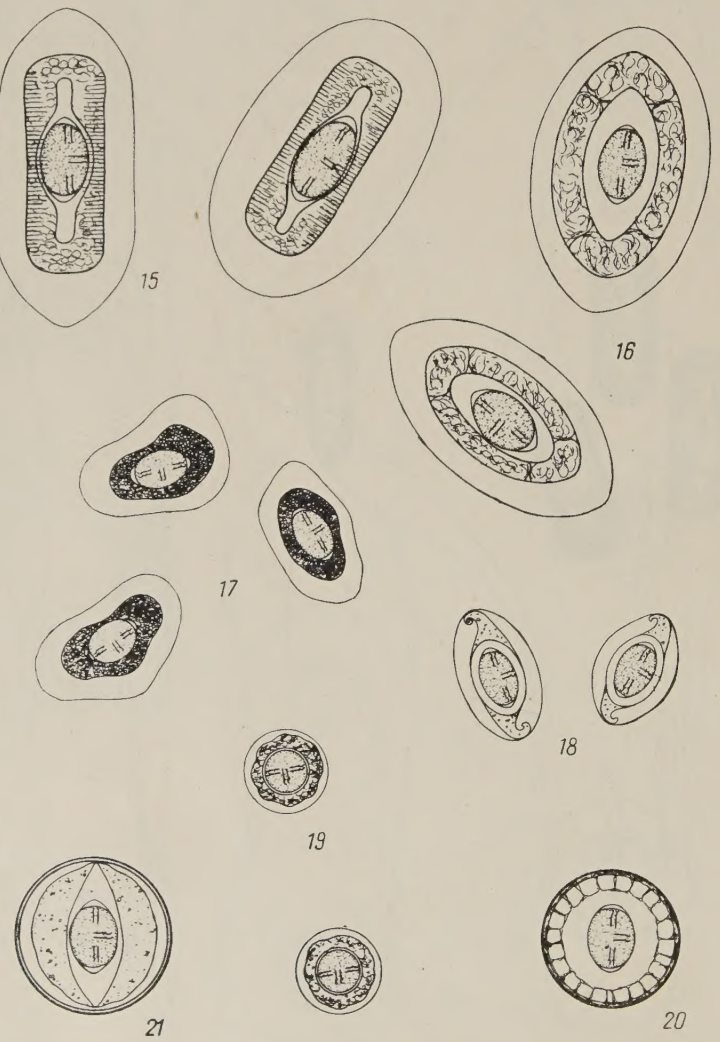
The internal egg membrane has double contour lines and is less transparent; it contains small, glittering granulations and in many species it has a more or less distinct structure. The structure of the internal egg membrane



Eggs of: 11 — *Diorchis nyrocae;* 12 — *Diorchis* sp.; 13 — *D. inflata* (after Rybicka 1947); 14 — *D. ransomi* (after Rybicka 1947)

in *Hymenolepis macrocephala* is granular (Fig. 17), and in *Tatria acanthorhyncha* is reticular (Fig. 8). The internal membrane of *Diorchis stefańskii* eggs is ribbed-like, similarly to some *Diatomeae* (Fig. 15). The structure of this membrane in *Hymenolepis megalops* eggs resembles a simple epithelium, and together with the adherent external egg membrane it resembles a simple cover epithelium of plants (Fig. 20).

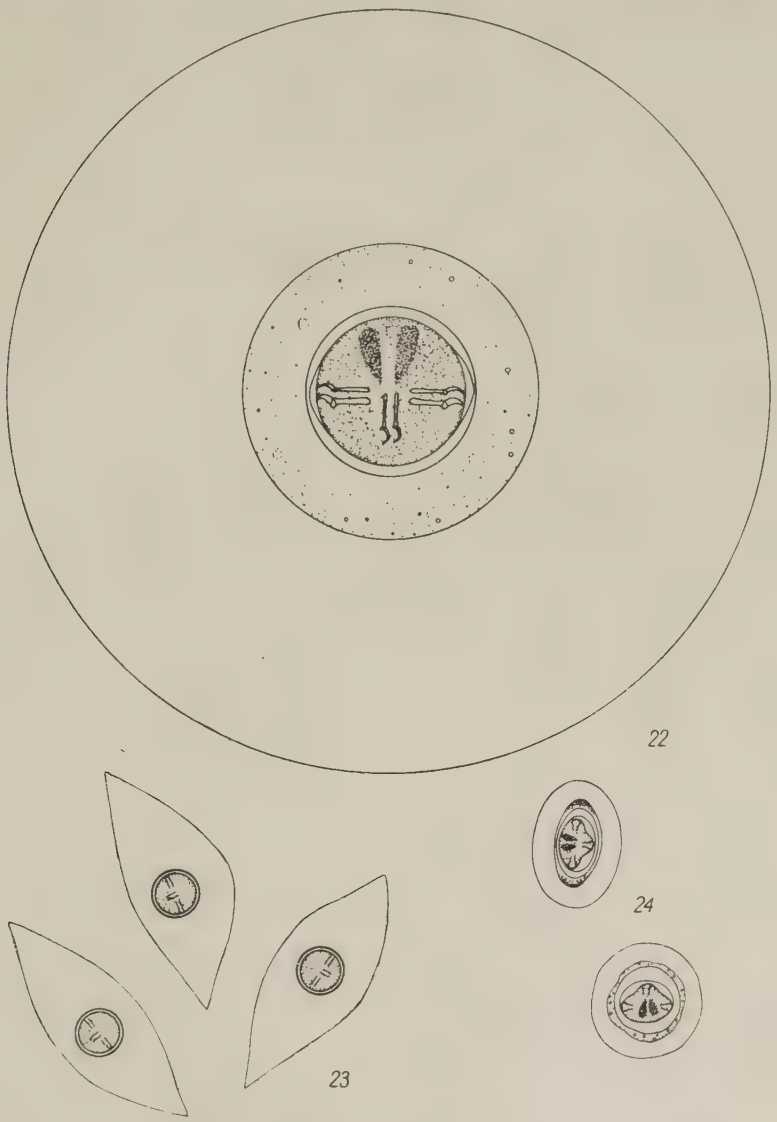
The shape of the internal membrane and its thickness also point to considerable differences in various species. Eggs of many tapeworms have that membrane relatively thick the shape of which is near the spherical one, e. g.,



Eggs of: 15 — *Diorchis stefańskii*; 16 — *D. parvogenitalis*; 17 — *Hymenolepis macrocephala*; 18 — *H. aequabilis*; 19 — *H. gracilis*; 20 — *H. megalops*; 21 — *H. sacciperium*

in the eggs of *Hymenolepis compressa, H. paracompressa, Diploposthe laevis* and in others presented on plate I. There are cylindrical internal membranes in the eggs of *Diorchis stefańskii, D. parvogenitalis* and *D. nyrocae* (Fig. 11, 15, 16), or spindle-shaped, with their ends twisted in opposite directions, in *Hymenolepis aequabilis* eggs (Fig. 18).

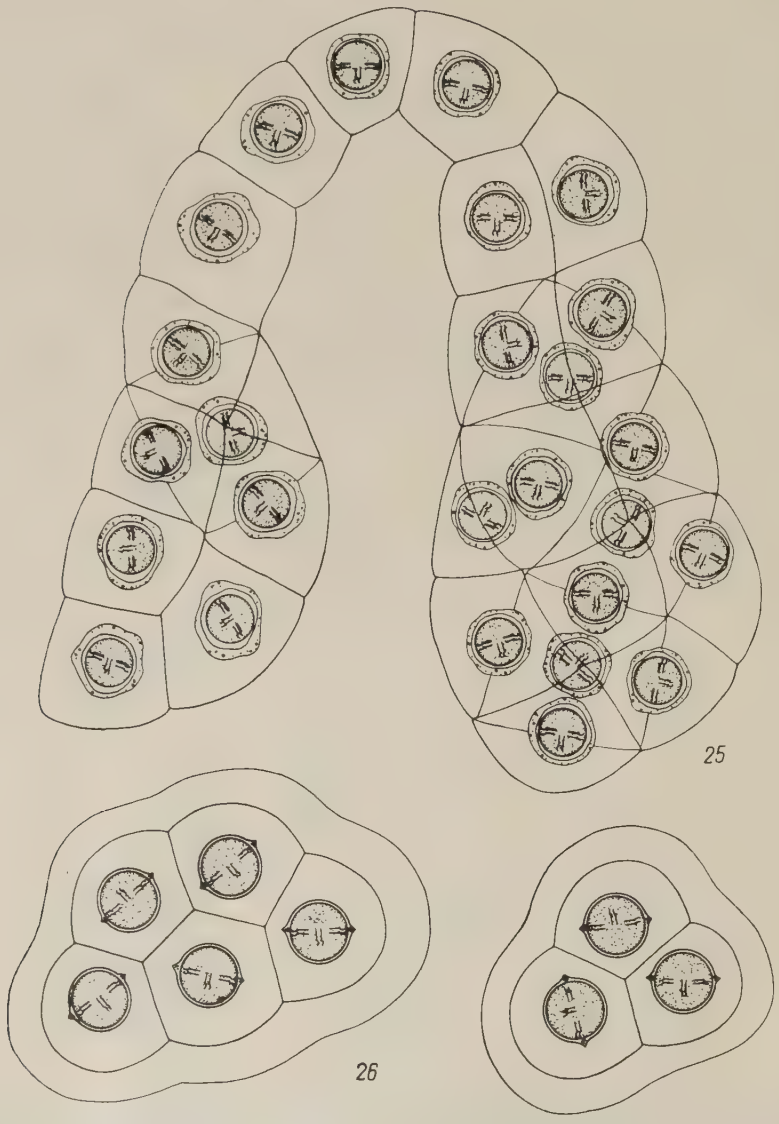
Most frequently the internal outline of the internal membrane has a different appearence than the external one. It has been shown by the drawings



Eggs of: 22 — *Paricterotaenia porosa*; 23 — *Anomotaenia ciliata*; 24 — *Hymenolepis furcifera*

of *Diorchis stefańskii* and *Fimbriarioides intermedia* eggs (Fig. 1, 15). The internal egg membrane does not generally adhere to the oncosphere membrane, but the space between them is filled with a transparent substance.

The oncosphere membrane is a very thin and transparent spherical or, more often, slightly oval film. This membrane can be hardly observed because of its thinness and because it adheres to oncosphere. It is visible clearer in *Hymenolepis furcifera* eggs the oncospheres of which are mobile (Fig. 24), as well as in the triangular-shaped oncospheres as, e. g., in *Tatria acantho-*



Eggs of: 25 — *Hymenolepis abortiva;* 26 — *Aploparaksis furcigera*

rhyncha (Fig. 8). In many species the oncosphere membrane is visible on the poles of oncospheres ovals.

The size of oncospheres and the length of the embryonal hooks also show certain differences in various species. Relatively small oncospheres (*Anomotaenia ciliata, Hymenolepis furcifera* and *H. macrocephala)* are 20 μ in diameter; relatively big oncospheres (*Diploposthe laevis* and *D. sui-generis*) are 36 — 40 μ in diameter. Oncosphere of *Paricterotaenia porosa* is 95 μ in diameter.

The embryonal hooks have the same shape in all species described in the present paper with the exception of *Paricterotaenia porosa* and *Hymenolepis abortiva*. The embryonal hooks of these species are differentiated similarly, though their length is different; namely the middle pair of hooks has a different shape than the lateral one, and both hooks of the lateral pair also differ from each other. One of those hooks is thicker and more solid (Fig. 22, 25).

The length of the embryonal hooks of the majority of species ranges from 9 to 11 μ. Relatively big hooks which are 16 μ long, are present in oncospheres of *Diploposthe laevis* and *D. sui-generis*. The embryonal hooks of *Paricterotaenia porosa* are very big (30 μ) whilst those of *Anomotaenia ciliata* are very small (6.5 μ).

Beside the great variety of shapes and dimensions (the drawings of eggs were done by keeping a uniform proportion), the eggs of some tapeworms are heavy and are going down in water, whereas others are light and swim passively by slight water movements because their weight is nearly the same as the specific weight of water. As an example of heavy eggs are those of *Hymenolepis megalops* and *H. sacciperium*, and of light eggs those of *H. furcifera, H. macrocephala, H. paracompressa, H. spiralibursata, Anomotaenia ciliata, Diploposthe laevis* and *Fimbriaria fasciolaris*.

In two tapeworm species I also observed some colouring of eggs. The *Hymenolepis sacciperium* eggs are brownish, those of *H. megalops* are rosy and opaline.

4. Morphological adaptations of eggs in the life cycles of tapeworms

Among many adaptations of parasites to their way of life and developmental conditions, the morphological adaptation of tapeworm eggs in their life cycles has not been known so far. It resulted undoubtedly in being not acquainted with the intermediate hosts of a great majority of tapeworms and in the lack of descriptions of live eggs observed in natural environment in which they accomplish their biological function of invading the intermediate hosts.

A further development of a tapeworm from the order *Cyclophyllidea* can follow only by swallowing of an egg by an intermediate host, in the body cavity of which the invasive larva for the final host develops. In the tapeworms examined by me the invasive eggs were spread in water by the final hosts. The intermediate hosts of those tapeworms are fresh-water invertebrates mainly *Copepoda, Ostracoda, Cladocera* and *Oligochaeta*.

Kisielewska 1959 studies on the development of *Drepanidotaenia lanceolata* (Bloch), as well as my own studies on life cycles of the tape-

worms parasitizing water birds, the result of which have been summarized in the present work, show the existence of specificity in reference to the intermediate hosts of those tapeworms. In other words, the particular tapeworm species are adapted to their development only in the particular *Crustacea* species. That specificity can be of various range and it is undoubtedly the result of physiological adaptations like resistance on the action of digestive juices and the ability of development in the body cavity, as well as the ecological adaptability conditioning the contact in natural conditions between the intermediate and final hosts. The contact between the intermediate hosts and the tapeworm eggs takes place in water, in my cases in the lake.

The studies on morphology of tapeworm eggs, as well as on their intermediate hosts, showed that the rich morphological variety of eggs (variety of shape, size and weight) has its biological basis. It is an expression of adaptation that enables the passive oncosphere to find its way in the highly differentiated lake environment (especially in the lithoral zone) to the proper, often specific invertebrate species. It is not only an adaptation to life in water where an egg is waiting until it gets swallowed accidentally by an invertebrate, but it is an adaptation enabling the contact with the proper intermediate hosts in which further development of the tapeworm can follow.

As my observations have shown, those adaptations enable eggs the stay or finding their way to environments of intermediate hosts and find an expression in conformity of shape and size of eggs to the forms being the natural food of intermediate hosts.

The adaptation to a biotope is the sinking of heavy eggs of *H. megalops*, where the host is the benthal ostracode *Cypris pubera*. The floating eggs of *Anomotaenia ciliata*, *Hymenolepis furcifera*, *H. paracompressa*, *H. spiralibursata* and many others are accessible to the swimming *Copepoda* and *Cladocera* species. An example of adaptation to the biotope are also the filiform eggs of *Diorchis inflata*, *D. ransomi* and *D. nyrocae* (Fig. 11, 13, 14). The intermediate hosts of those tapeworms are two *Ostracoda* species: *Cypridopsis vidua* and *Cyclocypris laevis*. During the studies on their natural invasion I observed that the occurrence of those *Ostracoda* species was connected with *Ceratophyllum*. Its shape suits them to settle on the little needle-shaped leaves of that plant and owing to that they can be eaten by ostracods which feed on those leaves.

As I have pionted out, the adaptations find an expression in conformity of eggs to forms being the natural food of intermediate hosts simultaneously with the adaptations enabling eggs the stay in biotopes of intermediate hosts. The tapeworm eggs are similar to algae, protozoans, or persistent forms of plants and animals (see figures).

Those similarities find an expression in the size and shape of eggs. The possibility of swallowing an egg is conditioned by its size (e. g., too big eggs of *Hymenolepis compressa*, *Diploposthe laevis* and of other tapeworms cannot be eaten by *Cladocera*), but the attractiveness of eggs for the corresponding invertebrate species is conditioned by their shapes.

The intermediate hosts of *Hymenolepis furcifera* and *Anomotaenia ciliata* are the lithoral species of *Cladocera*. They can be eaten by *Cladocera* because of the small egg dimensions of those tapeworms and their very thin external membranes (Fig. 23, 24). The relatively big and swimming spherical eggs of

Hymenolepis compressa, H. spiralibursata, H. paracompressa and *Diploposthe laevis* (Fig. 1, 3—9) are eaten by the big lithoral species of *Copepoda*, as *Macrocyclops albidus* and *Acanthocyclops viridis*.

The big and relatively heavy egg packets of *Aploparaksis furcigera* and *Hymenolepis abortiva* can be eaten only by the bigger (than plankton *Crustacea*) fresh-water invertebrates (*Oligochaeta, Amphipoda*) being at the same time very attractive for them as food. A great number of oncospheres contained in the packet finds simultaneously conditions for the development in the body cavity of *Oligochaeta* segments in the case of *Aploparaksis furcigera*, or in *Gammarus* sp. in the case of *Hymenolepis abortiva* (Fig. 25, 26).

The shape of the internal egg membrane of the tapeworm eggs of genus *Diorchis* are similar to *Diatomeae*. At the same time I observed that food of *Ostracoda* is partly composed of *Diatomeae*. The internal membrane of *Diorchis stefańskii* eggs is even striped delicately (Fig. 15) what is similar to the stripes of *Diatomeae* which were found in the alimentary tract of *Dolerocypris fasciata*.

The adaptive character of morphology of tapeworm eggs is also shown by the general observation that tapeworms having similar shapes and sizes of eggs develop in the same species of fresh-water invertebrates or in species with similar biology. On the other hand the more the shape of tapeworm eggs is specialized, the narrower is the range of specificity observed in relation to intermediate hosts. It seems that it agrees with the general principle of adaptation that species with stronger adaptation also demonstrate a narrower specificity what has been formulated by Raabe 1947 while analysing the morphological adaptations of *Ciliata* to the parasitic way of life.

Eggs similar in shapes and sizes are of the following tapeworms: *Hymenolepis compressa, H. paracompressa, H. spiralibursata, H. paramicrosoma, Fimbriarioides intermedia, Diploposthe laevis, D. sui-generis* and *Tatria acanthorhyncha* (Fig. 1, 3—9). The main intermediate host of the mentioned tapeworm species is *Macrocyclops albidus*. Besides, they can also develop in other lithoral species of *Copepoda* as *Acanthocyclops viridis, Macrocyclops fuscus, Eucyclops macruroides, E. macrurus, E. serrulatus* and *Mesocyclops leuckarti*.

Here can be also included examples from the literature concerning live eggs which develop also in *Copepoda*, e. g., *D. lanceolata* (described by Ruszkowski 1932), *H. fasciculata* and *H. setigera* (described by Paruchin 1954), and *H. vistulae* (described by Czapliński 1960). Even eggs of *Proteocephalus percae*, a tapeworm of fishes, are also similar. The intermediate host of this tapeworm is *Eudiaptomus graciloides*.

All those eggs form a group of similar eggs and we can add that they are characteristic for tapeworms the intermediate hosts of which are *Copepoda*. It is worthwhile noticing that the majority of *Copepoda* species possess similar biology and due to that there occurs a less distinct developmental specificity for the particular species of those *Copepoda*.

To the second group of eggs with similar shapes and sizes belong without any doubt the eggs of *Diorchis nyrocae, D. inflata* and *D. ransomi* (Fig. 11, 13, 14). The intermediate host of those tapeworms is *Cypridopsis vidua*, and also *Cyclocypris laevis* for *D. ransomi* and *D. nyrocae*.

Two other species of the genus *Diorchis: D. stefańskii* and *D. parvogenitalis* have similar eggs (Fig. 15, 16), but they differ in shape and size from

the eggs of the above mentioned species; there are also occurring other intermediate hosts. The intermediate host of *D. stefańskii* is a big ostracode *Dolerocypris fasciata*. The experimental contact of *D. stefańskii* egg with *Cyclocypris laevis* and *Cypridopsis vidua* has shown that both species cannot be the intermediate hosts of that tapeworm. *Cyclocypris laevis* did not eat the eggs of *D. stefańskii* and *D. parvogenitalis* which were probably too big; oncospheres of *D. stefańskii*, however, passed into the body cavity of *Cypridopsis vidua*, but they did not find conditions for further development (Jarecka 1958a). Though *Cypridopsis vidua* is an experimental intermediate host for *Diorchis parvogenitalis* I suppose that it does not play the part of the intermediate host in natural conditions.

Tapeworm eggs the intermediate hosts of which are *Ostracoda*, contrary to eggs developing in *Copepoda*, are heteromorphous and show developmental specificity in relation to the particular *Ostracoda* species. *Cypridopsis vidua* is the intermediate host for *Diorchis inflata*, *D. nyrocae* and *D. ransomi*, but is not for *D. stefańskii*, *Hymenolepis megalops*, *H. macrocephala* and *H. aequabilis*. *Cyclocypris laevis* is the intermediate host for *D. nyrocae*, *D. ransomi*, *Hymenolepis aequabilis* and *Dicranotaenia coronula*, but it is not for *D. inflata*, *D. stefańskii*, *D. parvogenitalis*, *H. megalops* and *H. macrocephala*. *Notodromas monacha* is the intermediate host for *H. macrocephala*, *Dolerocypris fasciata* for *D. stefańskii*, *D. coronula* and *H. gracilis*.

The example of tapeworms developing in *Ostracoda* makes it visible that the more specialized is the shape of those eggs, the narrower is the specificity in relation to *Ostracoda* species. *Diorchis stefańskii*, for example, develops only in *Dolerocypris fasciata*, *Hymenolepis megalops* only in *Cypris pubera*, and *Hymenolepis macrocephala* only in *Notodromas monacha*.

The distinctly marked specificity in relation to *Ostracoda* species has undoubtedly a connection with the differentiation of biotopes of *Ostracoda* in natural conditions. During my investigations on the natural invasion I noticed that *Ostracoda* species did not occur together. I had to find places in which those species were present. As a guide in this case were plants. The occurrence of, e. g. *Cypridopsis vidua* was connected with *Ceratophyllum*. *Dolerocypris fasciata* was found on moist meadows and on lake flood-plains where there grew plants of the genus *Rumex*. *Cypris pubera* occurred in spring in flooded plains and in small bodies of water near to the lakes. *Notodromas monacha* was found only in some lithoral places which I cannot characterize more closely. In the examined lakes the most common species as to its number and its occurrence as well was *Cyclocypris laevis*. These ostracodes occurred amidst the bushes of *Ceratophyllum*, frequently with *Cypridopsis vidua;* amidst three-leaved duck-weed together with *Copepoda* and in many other euthropic lithoral places.

The intermediate hosts for the majority of tapeworms examined by me are *Copepoda* and *Ostracoda*, whereas *Cladocera* are only for *Hymenolepis furcifera* and *Anomotaenia ciliata*. The eggs of those tapeworms are relatively very small and light and have a very thin external egg membrane (fig. 23, 24).

The eggs of *Aploparaksis furcigera*, *Hymenolepis abortiva* and *Fimbriaria fasciolaris* are joined in packets. The intermediate host of *A. furcigera* is *Lumbriculus* sp., that of *Hymenolepis abortiva* is *Gammarus* sp. We may sup-

pose on that ground that the intermediate hosts of tapeworms, the egg of which are joined in packets, are fresh-water invertebrates of larger sizes than *Copepoda, Ostracoda* and *Cladocera,* e. g., *Oligochaeta* or *Amphipoda* and possibly the larvae of *Insecta.*

The intermediate hosts of *Fimbriaria fasciolaris* according to my invastigations are *Copepoda,* but G a r k a v i 1950 says that he has found cysticercoids of that tapeworm in *Gammarus* sp. It is possible that this tapeworm can develop both in *Copepoda* and in *Amphipoda* but its eggs because of their lightness and shape of the internal egg membrane approximate with their general characteristics to the tapeworm eggs developing in *Copepoda.*

Dealing with the problem of morphological adaptation of tapeworm eggs I find it proper to reserve myself against too categorical and schematic interpretations. We ought to bear in mind that biology of the intermediate host has not been sufficiently known and we have also a small knowledge as regards the specificity of their food.

Nevertheless the observation that tapeworms with similar eggs develop in the same or closely related fresh-water invertebrates has reached such a degree of accuracy that it became very helpful in my invesigations when searching for intermediate hosts. I think that it can be applied in further investigations as a guiding scheme.

There is no doubt that the problem of morphological adaptation of tapeworm eggs is connected with the problem of specificity in relation to the intermediate hosts. We must admit that in the formation of the intermediate host — final host system there played a part not only the egg morphology but the physiological factors as well, e. g., resistance of oncospheres to digestion and ability of development in the body cavity, as well as the phylogenetic and ecological connections of tapeworms and their hosts. At present it is difficult to explain which of those factors in the history of development of the particular tapeworm species were of primary importance. The specificity of the intermediate hosts of tapeworms is surely the result of a number of morphological, physiological and ecological adaptations.

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STRESZCZENIE

Na podstawie zbadanych cyklów rozwojowych 28 gatunków tasiemców należących do rodziny *Hymenolepididae* Fuhrmann 1907 autorka rozpatruje zagadnienie morfologicznej adaptacji jaj tych tasiemców do warunków rozwojowych.

Autorka stwierdza, że bogata różnorodność morfologiczna (różnorodność kształtów, wielkości) jaj różnych gatunków tasiemców jest wyrazem adaptacji, która ułatwia zawartej w jaju onkosferze trafienie do odpowiedniego gatunku bezkręgowca, w którym tylko może nastąpić jej dalszy rozwój. Morfologiczne adaptacje umożliwiają jajom tasiemców przebywanie w biotopach żywicieli pośrednich oraz znajdują wyraz w upodabnianiu się kształtów i wymiarów jaj do form stanowiących naturalny pokarm żywicieli pośrednich.